THE LARVA AND SPAT OF THE CANADIAN OYSTER

J. STAFFORD, M.A., PH.D.
McGILL UNIVERSITY

II. THE SPAT

IN the first part of this article, dealing with the larva,[1] I have already indicated that, in the progress of my research, it soon became necessary to plan means of procuring young oyster spat for comparison with my supposed oyster larvæ before I could feel satisfied that the latter were in reality larvæ of the oyster. Of the common bivalve mollusks only Ostrea and Anomia live fixed to objects of support, so that the matter has some appearance of simplicity in the fact that all free-living forms may be eliminated. But careful examination of eel-grass, rock-weed and other marine plants, of shells, stones, timbers and other objects revealed no young spat, and I was forced to wonder where the oyster secreted itself at this stage of its life. I examined sand with the microscope to find if, like many bivalves, the young oyster might burrow for a time, but with no better result. Bundles of brush were tied to submerged rocks, or weighted with stones and sunk at various places. These were examined at intervals but without success. Each failure suggested some new possibility that required examination and occasioned delay. Time was flying, it was getting late in the season, and each day brought no further progress. What stupendous obstacles present themselves to the investigator and how simple after one has once mastered them!

A copy of Jackson's work,[2] procured for me at this time by Professor Wright, was particularly opportune, and I owe to it much by way of information and suggest-

[1] AMER. NAT., XLIII, Jan., 1909, pp. 31–47.
[2] See literature 12 of part I.

EXPLANATION OF PLATE

The plate accompanying "I. The Larva" was intended to be lithographed of the same size but was reproduced smaller and lost detail. I find from measurements the figures are magnified about 30 diameters. To agree with it the figures 1, 2, 3 of this plate, "II. The Spat," are magnified 30 diameters.

FIGS. 1, 2, 3. Young spat of Canadian oyster from the right (upper) side as they occur attached. Magnified 30 diameters.

FIG. 1. Oyster spat .5 mm. high, showing larval and spat shells.

FIG. 2. Spat 1 mm. high. The larval shell grows no larger, the spat shell grows to the adult size. Many organs are sketched in but the liver is left out, as it would obscure other parts.

FIG. 3. Spat 1.5 mm. for comparison.

FIGS. 4–12. Transverse sections of oyster spat 1 mm. high (compare Fig. 2), viewed from behind so that left and right of the figures correspond with the observer. The sections are in order from anterior to posterior but are not successive. The shells had been decalcified and are somewhat diagrammatic, thin left and thick right valve.

FIG. 4. Section through region of upper lip and transversely to anterior filaments of left inner hemibranch.

FIG. 5. Through mouth, unmarked parts same as preceding. The lower lip is borne by the anterior end of the abdomen (region of the foot).

FIG. 6. Mouth open at right, closed in to œsophagus at left. Rudiments of upper and lower palps.

FIG. 7. Œsophagus and tips of filaments of right inner hemibranch.

FIG. 8. Abdomen with five liver-follicles about the œsophagus.

FIG. 9. Through center of stomach showing œsophagus about to enter it, origin of intestine and right and left stalks of liver. Three other liver follicles are shown as well as the inferior lobe of the stomach, the visceral ganglia and the left inner hemibranch.

FIG. 10. Through anterior edge of adductor muscle, posterior end of gill.

FIG. 11. Through adductor and tip of inferior lobe of stomach. Several liver follicles.

FIG. 12. Posterior edge of adductor with rectum descending.

FIGS. 13–18. Transverse sections of spat 2, 2.5, 3, 3.5, 4, 5 mm. high. Not equally magnified. Left valve often damaged or left attached.

FIG. 13. Through mouth of 2 mm. spat, showing labial palps.

FIG. 14. Section of 2.5 mm. spat, touching anterior edge of adductor, showing the supra-branchial slit leading out from the supra-branchial cavity on the right side and the rudiment of the right outer hemibranch. Right and left inner filaments are cut longitudinally.

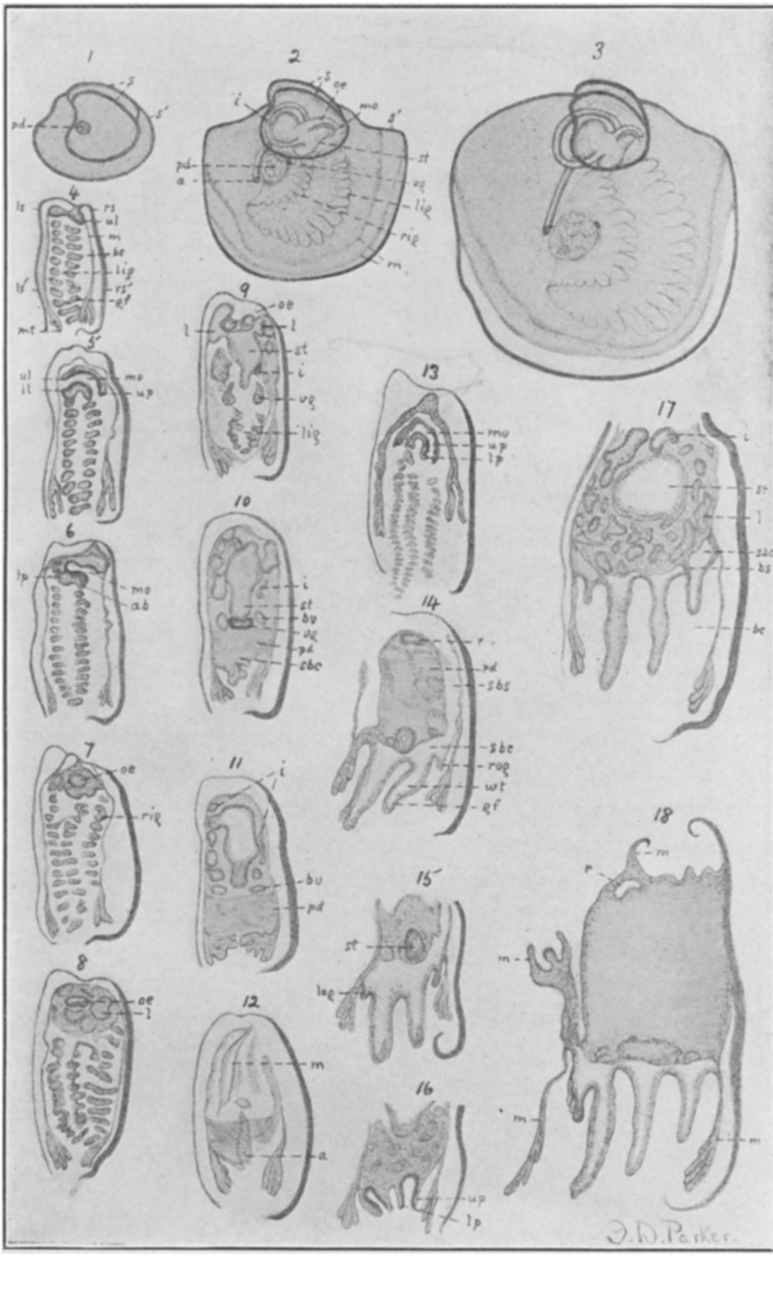
FIG. 15. Similar section of 3 mm. spat but slightly in advance and cut short above, showing rudiment of left outer hemibranch.

FIG. 16. Slightly behind mouth of 3.5 mm. spat, cut off above, to show all four labial palps. Liver follicles and portion of stomach above.

FIG. 17. Through 4 mm. spat, showing septa between supra-branchial cavities of inner and outer hemibranchs, the position of the original ctenidial axis.

FIG. 18. Section of 5 mm. spat through adductor muscle and visceral ganglia. The upper free edges of the mantle right and left of the rectum are very irregular. The branchial septa stop short of this section so that the supra-branchial cavity is continuous above all four hemibranchs.

a, anus; *ab*, abdomen; *bc*, branchial chamber; *bs*, branchial septum; *bv*, blood vessel; *gf*, gill filament; *i*, intestine; *l*, liver, *lig*, left inner hemibranch (gill); *ll*, lower lip; *lp*, lower labial palp; *ls*, left valve of prodissoconch (larval shell); *ls'*, left valve of dissoconch (spat shell); *m*, mantle; *mo*, mouth; *mt*, mantle tentacle; *oe*, œsophagus; *pd*, posterior adductor muscle; *r*, rectum; *rig*, right inner hemibranch (gill); *rs*, right prodissoconch; *rs'*, right dissoconch; *s*, prodissoconch; *s'*, dissoconch; *sbc*, supra-branchial chamber; *sbs*, supra-branchial slit; *st*, stomach; *ul*, upper lip; *up*, upper labial palp; *vg*, visceral ganglia; *wt*, water tube.



J. D. Parker.

iveness. The method of putting out glass[3] for the reception of fixed forms of animal life I had already become acquainted with at St. Andrews while working on the clam, but the present was the occasion to try every means that could be devised and quickly applied. I accordingly took what objects could be easily procured and constructed and set out traps calculated to capture full-grown larval oysters at the time of their fixation. The idea is the same throughout all forms of the method; the particular turn in application was my own. Window-glass was cut into strips 2×6 inches so as not to be too big to use on the stage of a compound microscope, the advantage of glass being that one can use either transmitted or reflected light and can turn it over so as to see, through the glass, the attached side of the oyster. These strips were stood on end in deep crocks, about a dozen in each crock, and kept from falling against one another by wire racks, the object of placing them vertical being to minimize the aggregation of sediment on their surfaces. The traps were then planted at various places where there were oysters—off Curtain Island where the oysters were large, and off Ram Island Point where there were many sizes of young oysters. The crocks were sunk in gravel just below low-tide level and made secure against the buoyant force of water and the lateral action of waves and currents by building stones around them but leaving the tops open. It was thought that larvæ, either swimming about or swept about by the waves, might drop into the crocks where the water would be comparatively still and find it easy to cling to the glass during the first stages of fixation.

Ram Island Point appeared to be the most favorable place and that was about six miles from the station, but daily visits were made, the strips of glass were one by

[3] Ryder, Comm. Fish. Maryland, 1881, p. 57; Bull. U. S. Fish Comm., 1882 (1883), p. 383. Horst, Bull. U. S. Fish Comm., 1882 (1883), p. 165; Rep. U. S. Fish Comm., 1884 (1886), p. 906. Möbius, *Zool. Anz.*, Jan. 22, 1883. Winslow, Bull. U. S. Fish Comm., 1884, p. 354. Jackson, *Science*, 1888, p. 230 (Vol. XI, No. 275); *Mem. Bost. Soc. Nat. Hist.*, 1890, p. 285.

one withdrawn and examined with a lens, and whenever a suspicious looking speck was observed the glass was put in a pail of sea-water and taken to the station to be examined with a compound microscope.

The strips soon became dirty, receiving a slimy coat speckled with sediment, plants and animals. There were bacteria, diatoms, algæ, protozoa, sponge-spicules, hydroids, polyzoon-colonies, worm-larvæ, crustacean larvæ, small snails, etc. It seemed as if everything but oysters could be obtained. So far as I saw, I had neglected nothing that might contribute to the result in view. Could it be that my suspected larvæ were not oysters, that there were no oyster larvæ or oyster eggs in the water! Once more I was bewildered.

At length, on the sixteenth of August, I discovered a single minute oyster-spat, bearing unmistakable marks of recognition and enclosing within the lately deposited spat-shell the prodissoconch of the free-swimming larva. On the nineteenth I found a second (Fig. 3), and on the twenty-second a third (Fig. 1). Everything speedily became clear. My experiments had been running ahead of nature. Oyster larvæ had been in the water, but they were not ready to transform into spat. They had to wait their time. On the thirty-first of August a fourth was taken.

After finding the first oyster-spat on glass I at once directed increased attention to natural marine objects and on the second of September I found a spat on the surface of a half-grown oyster-shell. From this time forwards they were to be found in increasing numbers and on various objects and, after being once shown them, the deck-hands of the steamer *Ostrea* could also find them. I have found spat on the shells of the oyster, mussel, clam, quohog, bar-clam, razor-clam, round whelk and on stones, but they must occur on many other objects as well. Judging from the numbers of half-grown oysters that carry periwinkle-shells at their umbos, it would seem that the periwinkle is a common base of fixation, although I did

not succeed in finding any with young spat attached. The dark color of the winkle, of course, makes it easy to overlook the smallest spat, and besides, these shells are frequently speckled or spotted with plant colonies such as *Ralfsia verruscosa,* the small colonies of which may simulate young oyster-spat in size, shape and color. One can distinguish the difference with a lens or by feeling them with a knife-blade. The young of *Crepidula formicata,* a low conical-shelled gastropod, is sometimes more difficult to distinguish, but with a knife-blade one can slide it along the base of attachment or pry it off and note that there is no under shell but a broad clinging and creeping foot. Anomia is one of the closest relatives of the oyster, but, from its shape and color, is usually not difficult to distinguish. Upon prying it off, the thin lower valve of the shell can be seen to have a hole through which a short stalk of attachment passes and permits movement. The oyster becomes fixed by means of a secretion, presumably from the edge of the mantle, which cements the left valve close and fast to the supporting rock or shell.

The spat caught on glass did not, of course, occur in regular order of progression in size: the first measured .87 × 1.03 mm. in height and length, the second 1.58 × 1.20, the third .51 × .55, the fourth .86 × .95. Similarly the first found on an oyster shell measured 2.4 × 2.3, while those subsequently procured varied from less than 1 mm. to 6 mm. in height.

The shell of the larva is longer than high, and this is true not only for each valve but also for the whole shell, even when the far umbo, through tilting of the shell, stands up above the near one. The youngest spat agree also with this statement, but when about 1 mm. in height the proportions become reversed, and from this time forwards the shell grows fastest below and at the postero-inferior angle. On this account it is more useful at first to build comparative measurements on the height rather than on the length—the height, both for the larva and for

the spat, being the vertical measurement from the top of the umbo to the lowest level of the opposite edge when the prodissoconch is placed in the position of a creeping clam.

The spat caught on glass exhibited the characteristic color of the pelagic larva—the smallest varying towards pink, the larger towards brown. Those taken on opaque objects, on the other hand, presented a different appearance—instead of having a pink, reddish or brown coloration as one would expect from comparison with the larva, or, instead of having a white appearance as might be looked for by comparison with the older spat and adult oysters, they preserved a shining, dark, metallic lustre with a few faint radial lines. In the center of the dorsal region could be distinctly recognized the larval shell (prodissoconch) of the oldest free-swimming stage, presenting a uniformity of appearance in all the specimens, and measuring in the neighborhood of $.369 \times .384$ mm. in height and length.

The spat-shell (young dissoconch) is deposited by the thickened rim of the mantle in layers along the ventral and terminal edges of the larval valves, but not to any extent along the dorsal or hinge edge, which explains the concentric lines below the umbos. The latest deposited parts around the margins are very thin and delicate and exhibit a prismatic structure. At first the shape varies little from that of the prodissoconch, but soon the dissoconch becomes extended fore and aft of the hinge-area in a manner that suggests the wings (ears) of a scallop-shell, the lower parts preserving a pretty uniformly curved outline. Later these alæ cease to be conspicuous and the whole outline may become irregular and variable. Deep or shallow concentric creases preserve more or less indication of stages of growth, and at places may be portions of radial lines. The deeper concavity of the left valve remains noticeable for a time after fixation takes place, particularly in sections, but a little later the lower valve seems to lag behind the

upper one in growth, appearing thinner and flatter, while the upper one is thicker and more curved. At a still later period the growing edge of the lower valve becomes free and the valve again acquires a deeper cavity than the upper one, preserving this difference throughout life.

While the developing oyster is free to swim or to creep it is, of course, natural to describe it in terms suitable to such permanently free-living species as the clam. The more pointed end, that ordinarily precedes in locomotion and from which may protrude the velum or the foot, is the anterior end. The foot is postero-ventral to the velum. The umbos are postero-dorsal. The hinge is dorsal, *i. e.,* between and in front of the umbos. The longest diameter is horizontal, and the height is a vertical line at right angles to the length. With the growth of the spat it becomes difficult to retain such ideals as continuously useful marks of description. At periods varying somewhat with the individual they become more or less modified. Preserving the original orientation of the prodissoconch, the height of the dissoconch soon becomes greater than the length, the hinge and umbos come to mark the narrow anterior end of the spat, and the larval shell sinks into insignificance. Its left valve frequently becomes obliterated by growth of the surface of attachment, but its right valve may often be found until late in the life of the spat, although it is liable to become destroyed by weathering of the umbo-region. While its position marks the anterior end of the oyster, it has long since been carried up on the tip of the umbo of the dissoconch out of reach of the hinge or of the growing parts, but its anterior end still points in a general way in the direction of the anterior end of the adult. This position and relationship is correlated, as will be seen later, with the increase of growth of the lower and posterior parts of the oyster's body, which occasions more or less of a rotation round the great adductor muscle, and resulting in longer or rounder forms of shell with a straighter dorsal and a much curved ventral border.

The right, upper, valve remains flatter and smoother, the left, lower or attached valve, more deeply hollowed, rougher, with more conspicuous concentric furrows, and often with blue tipped projecting processes.

Note on the Asymmetry of the Shell.—In the free-swimming larva the greater convexity of the left valve can not be due to external conditions in the life of the larva since both valves are developed under like conditions, but must result from a cænogenetic modification of biogenesis, which is to say that the difference in the two valves was first developed after some remote but free and symmetrical ancestors of the present oyster took to a fixed mode of life, becoming attached by simply cementing the left valve fast to a solid substance upon which it rested, and that somewhat later in the phylogenetic development the hereditary transmission of this character became modified to precede, in the life of the individual, the conditions which originally called it into existence. It is conceivable that gravity was the prime incentive both to the occasion for fixation on one side and to the first asymmetry. Many other mollusks have been similarly modified, *e. g.*, Anomia, Pecten, Mya, deep-bodied animals that habitually fall over on one side as soon as locomotion ceases. When once developed there may have been an advantage in transmitting the lob-sidedness to earlier and earlier stages in the offspring, which could take place by natural selection. Such an advantage might well be the determining that the heavier left side of the larva, when settling to the bottom or when creeping movement ceases, should promptly come in contact with the point of fixation and insure the most favourable relative positions for the activity of other organs whose function had been perfected under like conditions in the adult. The temporary transfer of the greater convexity to the upper valve in young stages of the spat can be explained by the fact that for a time the growth of the lower valve follows, as it is cemented to, the surface upon which it rests, while the upper valve is free for growth in every direction. When a sufficient surface of attachment is secured the edge of the lower valve becomes free, and then the greater convexity soon reverts to the left valve again.

In living spat the mantle can be often seen protruding beyond the edge of the shell, but in preserved specimens it is retracted, sometimes close up to the gills and body, so that the soft parts of the animal may occupy only a half to a third of the cavity of the shell. In the youngest stages the margin of the mantle is thickened, and the beginnings of tentacular processes are present. Differences in the two sides afterwards become noticeable, such

as thickness, length, and the greater freedom of the right side from the body, where, for a considerable area in front of the adductor muscle, there is open communication from the supra-branchial chamber to the outside at the dorsal edge of the shell (Figs. 14, 15).

The anterior adductor muscle is present for a time in the spat, and appears to move upwards and backwards from its original position in the larva, until it is crowded to the edge and disappears before the oyster reaches 1 mm. in depth. The posterior adductor muscle, on the other hand, increases regularly in size and moves downwards and slightly backwards, leaving distinct lines on the shell to indicate its change of position. In spat .86 mm. high it is just below the edge of the prodissoconch (Fig. 2), in those 1.5 mm. high it is twice the depth of the prodissoconch from the top of the shell (Fig. 3); in all stages it is nearly in the median horizontal plane and slightly posterior to the median frontal plane. The movement may be effected by a slow creeping of the muscle, due to downward pressure from the growth of the body above, or by the addition of new fibers below and the absorption of old from above, while the impressions on the shell may result from the inability of the mantle to deposit new layers of pearly matter under the attached ends of the muscle.

Of the organs enclosed by the mantle a conspicuous part is early assumed by the gills. The oldest larva or the youngest spat has two of these—one on each side of the body, below and between the line of attachment of the mantle and the base of the foot. At this time each gill possesses a row of about eight filaments, of which the anterior are larger and more completely separated from each other, the posterior are shorter and only partly separated by vertical creases, while all are united above by an undivided longitudinal ridge or basal axis that projects behind and below the mass of the body. At the time of fixation the right and left gills are approximately equal, but when the spat reaches .86 mm. in height (Fig.

2) there are about sixteen long filaments on the left side and about ten short filaments on the right side—the left gill extending in front of and behind the right one and occupying most of the gill-chamber (Figs. 4–8). In spat of 2.5 mm. height there appears on the right side, outwards from the already present gill, a third series of minute, papilla-like filaments (Fig. 14), and when the spat reaches 3 mm. in height a fourth series is to be seen in the corresponding position on the left side (Fig. 15). They increase in size during the growth of the spat until the animal possesses four complete gill-leaves corresponding with those of the adult.

During larval development the gills of the oyster make but little progress towards the complicated structure of the adult. The free-swimming animal being small, respiration can for a time be partly subserved by its surface. But fixation effects a marked change in its mode of life and is followed by far-reaching modifications in its organization. Rapid increase of size demands improved facilities for respiration. But, as the animal no longer comes in contact with its food through swimming movements, it must depend upon the respiratory currents for bringing food to itself; hence the gills acquire a double importance. Moreover, since the conditions favorable to bilateral symmetry are interfered with, the equal balancing of right and left sides in the further growth of organs must be left to heredity. At the time of fixation, as we have seen, the gills are represented by two bilaterally symmetrical inner gill-leaves. The left (now under one) grows much faster than the right (now upper one) so that there is more room and less pressure above, facilitating the development of the right outer gill-leaf before the corresponding one of the left side. Irregularity also soon becomes noticeable in the higher level of origin of those of the right side and in a tendency towards a radial symmetry of the organs with reference to the posterior adductor muscle.

A study of sections of larvæ and young spat reveals

a remarkable difference in the apparent ontogenetic development of the gills of the oyster as compared with the recorded phylogenetic development in lamellibranchs. This, like the larval asymmetry of the shell, may be understood as a short-cut towards the final structure. As the first-formed, short, basal axes grow backwards they carry with them a continuation of the body-wall, connecting them with one another across the median sagittal plane and with the mantle at both sides, giving rise to a very imperfect separation into branchial and supra-branchial (or cloacal) chambers. The filaments are at first short, solid, papilla-like outgrowths from the axes —the older and larger anterior, the younger and smaller posterior. They originate behind, but by formation and growth of new ones those first formed become pushed forwards. The at first small and shallow supra-branchial chamber follows this movement and penetrates each filament from above, distending it laterally but not antero-posteriorly because of the pressure of contiguous filaments. This process continues until each filament is severed into an outer and an inner section, the intermediate portion becoming constricted through, but never completely at the tip. In this manner each gill-leaf becomes split into outer and inner lamellæ of similar structure, but the one the reverse of the other, with its parallel half-filaments and intervening slits overhung by cilia. Imperfect separation of the transverse median portions of the opposed halves of some filaments gives rise to the inter-lamellar junctions, while the imperfect separation of the opposed sides of different but contiguous filaments occasions the inter-filamentar junctions. The same process can be observed later in the development of the right and left outer gill-leaves as well as in the terminal filaments of any one of the four (Fig. 14).

For a long time it has been customary among zoologists to speak as if the oyster, or other bivalve mollusk, possesses four gills, which it really appears to do, two on each side of the body. Comparative study of the anatomy and of the development of different groups has led to the

view that bivalves have been developed from primitive, symmetrical, gastropod-like ancestors, with a simple head in front bearing two tentacles, two eyes, and mouth with a rasping tongue; a low conical shell above that could be drawn down over all the soft parts and lined by a mantle that secretes its material; a flat creeping and clinging foot below; and two feather-shaped gills, disposed right and left, projecting backwards. Each of these was a symmetrically constructed, bipectinate gill or ctenidium, having a central axis with two rows of filaments, an upper and a lower. There are still living limpet-like gastropods along our coasts possessing such characters, although no one species retains them all or in the most primitive form.

The group of mollusca to which the oyster belongs has in the course of time suffered modifications of the characters mentioned. Its members have taken to a more quiescent mode of life, such as burrowing in sand or fixing to rocks, and in consequence have largely lost those external organs of locomotion, plunder and special sense so necessary to free-roving animals. The absence of a head has been regarded as characteristic (hence the group has been called Acephala); in place of a single piece they have developed a shell with two valves (Bivalva); the foot in by far the greatest number of forms has become somewhat hatchet-shaped (Pelecypoda); the gills are leaf-like, each separable into flat plates (Lamellibranchia). If all bivalves had become equally modified it would certainly have been difficult to determine the origin of the group, but, owing to the diversity of natural conditions and the reactions of these upon living organisms, certain species have been forced to pursue special lines of action in order to better their chances for life, with the result that the organs chiefly concerned have become more specialized, while other organs have retained much of their original structure, and it is just these organs that are especially valuable in tracing ancestral affinities. As long ago as 1848 Leuckart (16) comprehended the essential unity of molluscan gills, and his views have been supported by Menegaux, Pelseneer, and many others. Peck has studied the Lamellibranch gill. Lankester, Hatschek, Thiele, Lang, are among those who have studied the phylogeny.

In the oyster larva one can at once recognize the ctenidial axis with its lower series of filaments, but one has to await the spat of 2.5 to 3 mm. before he can see the upper series, which has had to rotate outwards nearly half way round the axis in order to remain accommodated in the branchial chamber. In the adult there is but one gill on each side, comparable with a gastropod ctenidium and composed of two hemibranchs (gill-leaves or branchial foliæ); each hemibranch may be split lengthwise, from above nearly to the lower free edge but not through it, into outer and inner plates (lamellæ), or subdivided transversely into numerous V-shaped branchial filaments of which one half

belongs to the outer lamella and the other half to the inner lamella of a hemibranch.

In the course of phylogenetic development the originally straight filaments have become bent upon themselves to permit of greater length (surface) and still be protected within the branchial chamber—those of the ventral series were folded inwards and those of the dorsal (but now lateral) series were folded outwards, while the tips coming in contact with the foot in the one case or the mantle in the other clung for support, were directed upwards, and finally became fixed along the side of the body or along the inner surface of the mantle. At places their ciliated surfaces became knit together for further support, leaving intervening gill-slits between contiguous filaments, and ascending water-tubes between opposite lamellæ. At the level of union of the gills with the body and with the mantle there is separated off a branchial chamber below from a supra-branchial (or cloacal) chamber above, and by the activity of the cilia water is brought into the former, directed through the gill slits, up the water-tubes, and out by the cloacal chamber. The original ctenidial axis lies above the base of origin of each pair of hemibranchs, and is marked by retaining its connection with the body by a septum carrying blood vessels and nerves (Fig. 17).

Two larval organs soon disappear under the new conditions brought about by fixation: the velum and the foot. Even in certain old, free-swimming larvæ, that are perhaps belated in their efforts to become attached, a reduction in the size and vigor of the velum is noticeable. This would seem to suggest an atrophy of the organ, which might be followed by either dehiscence or absorption. I have occasionally seen old larvæ with the velum protruded and partly severed from the body, as well as completely separated vela still capable of muscular and ciliary movements. Such cases may have resulted from accidental pinching off by a snapping closure of the shell-valves. But the size, appearance, enfeebled movements, and even the accident itself, pointed towards an antecedent loss of ability to respond correlatively to the activity of neighboring organs.

Balfour (21, p. 215) states: "It has been suggested by Lovén, though without any direct evidence, that the labial tentacles of adult Lamellibranchiata are the remains of the velum. The velar area is in any case the only representative of the head."

Ryder (31, p. 404) says: "The detachment of the ring or crown

of vibratory filaments or cilia from the embryo as asserted by Davaine has not been confirmed by any other observer" and in 8, p. 790: "Davaine makes the statement that the velum appears to drop off sometime about the end of the larval period. Gerbe, on the other hand, asserts that the velum is transformed into the palps." This is a fascinating view of the destiny of the velum: that it does not become entirely useless and completely disappear, that its main line of folding in the median sagittal plane represents the division into two halves which bend around the sides of the mouth, each half again folding to form the two palps, while secondary radial foldings may give rise to the furrows and ridges and the cilia become redistributed. On the other hand it is not easy to see exactly how an organ of the size and shape of the velum could become reduced, remodelled, changed in position and folded in such a way as to form an anterior pair of palps, connected across in front of the mouth, and a posterior pair, connected behind the mouth and underlying the first, while the two on one side are attached along a line running back from the mouth and have their original ciliated surfaces turned towards each other. Moreover, this would mean a much more intimate connection between the epithelium of the velum and the inner walls of the mouth than exists in the larva, where the mouth-opening is surrounded by a funnel-shaped projecting rim, that is separated from the velum in front by a crease, while the lower lip is free to a still greater extent. There is no observable connection between the arrangement of cilia on the velum and on the palps, nor any positive antecedents of the furrows and ridges of the palps on the velum. Besides, from a consideration of the size of the velum in the larva and the size of the smallest recognizable palps in the spat, it would appear that the velum would have to suffer a period of decay followed by a period of vigorous growth. Restricting one's observations to the oyster it might seem just as likely that the lower palps should originate from the foot and only the upper ones from the velum. The foot is ciliated and has a median ventral furrow corresponding with the division-line between the lower palps. In that case one would expect to find vestiges of pedal organs, such as pedal ganglia and otocysts, about the bases of these palps under the œsophagus, as well as supra-œsophageal ganglia in the bases of the upper palps in front of the œsophagus. But in my sections I have not been able to recognize these structures, and reflection on other bivalves, where both foot and palps persist as functional organs in the adults, proves beyond doubt that the foot has nothing to do with the lower palps. I have three series of young spat-oysters with the shell measuring rather less than 1 mm. in height, and from a study of them I should say that the palps originate from, and belong to, the walls of the mouth, *i. e.*, are extended upper and lower lips.

The foot, after fixation of the larva, no doubt ceases to grow, perhaps becomes reduced, but in any case shrinks against, is absorbed into and incorporated with the anterior ventral wall of the rapidly enlarging abdomen. In 1 mm. spat it is scarcely recognizable as a median, grooved, muscular thickening between the lower lip and the first gill-filaments.

Jackson (12, p. 303): "The fact that a velum, or swimming organ, exists up to the period of permanent fixation accounts for the great reduction of the foot, because that organ is unnecessary while the animal is provided with another locomotive organ, and is useless for progression after the animal is attached. The reduction of the foot is clearly attributable to disuse and a high degree of concentration of development . . . seen so markedly in the development of the oyster." I have already shown, when dealing with the foot of the larva, that the part designated "foot" by Jackson and others is not the real foot, which is only to be found at a very much later period and which they had not recognized.

The intestinal system has all its parts represented in the larva. With the growth of the spat these suffer certain alterations in relative sizes, shapes, and positions. Perhaps the most radical change is produced by a rotation of the body in such a way that the mouth moves forwards and upwards towards the antero-dorsal margin of the prodissoconch. This doubtless accompanies and is associated with the loss of the velum, which in the larva is so large as to occupy all the fore part of the cavity of the shell, forcing the mouth and œsophagus backwards to near the median frontal plane of the body. In spat under 1 mm. in height when the velum is completely cleared away, the mouth can occupy its normal position as in the adult. Such a rotation may appear at first thought inexplicable, but when it is remembered that in the prodissoconch the body of the larva is possessed of great freedom of movement, being at times thrust far forwards, putting the retractor muscles on the stretch, it can be readily understood. In fact it is conceivable that these muscles may be made to do duty in producing the rotation and in fixing the body in its new

position, for after the loss of velum and foot there is no longer any need of such free movement, consequently these muscles may lag behind other parts in growth, exerting a tension as they do so sufficient to cause the rotation. In harmony with this view is the similar upward movement of the anterior adductor muscle and the rapid downward movement of the posterior adductor muscle.

In 1 mm. spat the two sides of the mantle, meeting above at a broad angle, appear to be suddenly thickened (Fig. 4) into a sort of upper lip for the widely open, transversely crescentic mouth, that opens a little farther back on the right side than on the left. The anterior end of the body, between the first gill filaments, serves as lower lip, while very short upper and lower palps, possessing only a couple of ridges and furrows, are continuous with the lateral margins of the upper and lower lips, and project on each side of the anterior end of the median left gill. In 2 mm. spat (Fig. 13) the palps have increased perceptibly, doubled the number of furrows, turned down, and are seen to be anterior to, but not continuous with, the gills. Judging from the great progress made between these two sizes, I believe that the palps originate sometime before the spat reaches 1 mm. in height, but are not present as such in the larva, where upper and lower lips and palps are represented by the internally-ciliated, funnel-like, projecting rim of the mouth. When this rotates upwards it comes to lie between the mantle above and the forward growth of the abdomen below, while its side-angles fold outwards and backwards becoming the palps, their like surfaces turned towards each other and their cilia continuous with that of the mouth and œsophagus. Later they become adherent to a greater extent along the lateral walls of the anterior part of the enlarging abdomen, and direct food from the gills into the mouth.

Rice (33, p. 28) curiously made the observation: "During the first period of attachment when the shell itself is not firmly attached, but simply held firmly down to the substance with which it is in contact,

the young animal gets its food, or a portion of it, by means of a sort of proboscis, or elongation of the mouth part, which is capable of being moved about freely within the shell cavity. This proboscis stage lasts until the gills are fully formed and becomes of sufficient size to supply food to the animal, when the proboscis, or rather its flexible end, is transformed into the labial palps which become closely connected with the gill-leaves."

The mouth narrows down into an œsophageal tube of transversely elliptical calibre, lined by cells similar to those of the mouth. It is still relatively long and curves over the anterior end of the stomach, passes between the lateral origins of the liver, and enters the stomach from above (Figs. 2–10). The stomach is a relatively large mass of irregular shape and large cavity, occupying a good part of the space in the prodissoconch. There may be considered to be three prominent extensions: one forwards below the œsophagus, another postero-dorsal behind the entrance of the œsophagus, and a third, beginning as a compressed ventral extension of the first, slants downwards and backwards towards the adductor muscle, becoming broad, deep, regular and thick-walled. This, I am satisfied, is the portion that secretes the crystalline style, and originates postero-dorsally in the left umbo of the larva, but becomes moved to its present position during the rotation of the viscera, and presents the appearance of being internally ciliated. Just in front of the insertion of the œsophagus but on each side of it, *i. e.*, dorso-laterally, spring the stalks of the liver—one on the left and two on the right. These branch into numerous follicles lying on both sides of and above the stomach and projecting far forwards to the region of the mouth. On the ventral aspect of the stomach, in the same region, springs the intestine, on the right, in the crease between the compressed antero-ventral extension to the left and the main central body of the stomach above (Fig. 9). From this the intestine passes backwards on the right, then upwards behind the rounded postero-dorsal extension, forwards and down the left side, where, near the anterior end of the stomach it turns

backwards and then down, finally passing towards the median plane to the anal opening over the adductor muscle. The stomach sometimes contains diatoms and desmid-like clusters of one to four nucleated cells.

The nervous, circulatory, excretory and reproductive systems remain undescribed, and shall not be treated of in this paper; they bear less important relations to those characters of external morphology and gross anatomy that are so useful as marks of recognition and description.

The first, second and third spat oysters caught on glass were of different sizes and were consequently devoted to morphology, but the fourth, being of approximately the same size as the first, was used for a physiological experiment in growth. This spat was procured on the afternoon of August 31 at Ram Island, about six miles from the station, and measured at 5 P.M. .861 × .953 mm. in height and length and had about sixteen gill filaments. It was kept under the bridge of Keir's wharf until the afternoon of September 1 and measured again, but it showed no increase of size. It was then taken to Ram Island and placed under its original conditions in a crock, and at 4 P.M., September 7, it measured 1.276 × 1.261 mm. and had about twenty-four gill filaments. It was kept in running seawater until 5 P.M. of the eighth and then put under the bridge of the wharf until the morning of the ninth, when it was again taken to Ram Island. It did not grow either in the running water or under the bridge where there is at times considerable tidal current. On the forenoon of the sixteenth it was again brought in and measured 1.753 × 1.661 mm. From these observations it would appear that the young spat did not become immediately accommodated to new conditions after being disturbed, that during a period of six days of undisturbed growth it increased to one and one half times its original height, and that at the end of seven days more it had grown to twice its original height. One might say that it doubled its height and length in two weeks.

Having to leave for Montreal by the twentieth, it appeared that the best thing left for me to do was to plan an experiment for the winter. I had three strong wire baskets made—two feet square by three inches deep and lids to fasten over—in which I placed perhaps three to four hundred small, selected, living oysters having one or more minute dark spat upon each shell, surrounded with circular lead-pencil marks for convenience in recognition. These baskets were connected by a long rope and put down in a deep channel between Hog and Bird Islands, presumably out of the way of fishermen, ice-shoves, etc. I expected the small dark spat, which varied from 1 to 4 mm. in height, to grow to about the size of one's thumb-nail during the winter and spring, as this was the size of the smallest white spat I recollected having seen upon first arriving at Malpeque the previous spring. The first thing I did the succeeding spring was to go and grapple for these baskets, but despite every effort they could not be found. The marks of the rope and baskets could be observed on the bottom, and the suspicion was near that some curious fisherman, in setting lobster traps in the early spring, had found them and taken possession for the rope—an illustration of the immediate short-sighted petty-selfishness and improvident disregard of impending wholesale benefits of many fishermen.

The next thing that suggested itself was to look for spat of the previous autumn on the shells where I collected those for the preceding experiment, and I was surprised to find dark spat still there, that had apparently not grown a bit or changed in color during the winter. There were fewer of them—many having died and lost the upper valve or even both valves were gone, leaving sometimes a patch or rim to indicate where a spat had been attached. The largest dark spat collected the previous autumn measured 6 mm., and the largest found the next spring was 8 mm. in height. They retained their dark metallic luster with radiating ridges

or lines and very thin edges—the whole oyster being thin and fitting so solidly against the supporting shell as to require some force with a knife-blade to separate it. In some of the larger was to be seen a tendency to turn white, in that the dark rays were irregularly separated by reversed lighter radiations. Sizes but little larger than these may be found later in the spring and in the early summer. The spat of the oyster-fishermen, varying mostly over one inch in length, are abundant, many barrels of which are collected by the Indians at Ram Island Point and thrown out off Lennox Island, the Indian reserve, for further growth.

Important results added to those given in the preceding part on the larva are:

19. First systematic use of plankton nets in the procuring of oyster larvæ.

20. First undoubted recognition of the larva of the oyster in Canada.

21. Stages hitherto unobserved (constituting the blank referred to by Jackson) may be taken in the plankton net.

22. The first undoubted recognition of young stages of Canadian oyster spat.

23. The spatting period has been limited.

24. The free-swimming period of life of the larva has been limited.

25. Size is a more useful criterion than age.

26. Sections have been prepared of both larvæ and spat in order to determine accuracy of structure.

27. The gills have been carefully studied.

28. The intestinal system has been described throughout.

29. Development has been followed up to adult sizes.

30. Many structural or other observations have been made, which to enumerate would be largely to rewrite foregoing pages.

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BRIEF NOTES AND EXTRACTS

Ryder (I. The Larva. Literature, No. 6, f. 3) and Jackson (No. 12, ff. 1, 2, 17, 18) have given figures of the youngest stages of oyster spat.

In the absence from the literature of any figures of the oldest free-swimming larvæ, I have already referred to these and for a more satisfactory understanding reduced their measurements to actual sizes. They represent the spat within 24 hours after fixation and measure in the neighborhood of .3 mm. in height. Ryder's Figs. 5, 4, 6, 7, represent spat of about .34, .38, .51, .54 mm. height. Jackson's Fig. 3 was perhaps about .55 mm. high and his Figs. 20, 21, about .91 mm. high. Then come Ryder's Fig. 8, about 1.6 mm., his (No. 8, p. 784) Fig. 2 of 3 mm., and Jackson's Fig. 4 of 5 mm. My youngest spat were .51 and .86 mm. high and from 1 mm. upwards I had such abundance I could select whatever sizes I desired.

On account of recorded differences between European and American oysters it is not always safe for us to judge from analogies. On the other hand, except for local differences of temperature, food, fauna, etc., the accrued knowledge of oysters in the United States is of immense value to Canada.

Importance of Embryological Study.—Winslow (No. 30, p. 234): "I would press the importance of continued investigation of the embryological life of the oyster. The effects of the various influences to which it and the mature animal are exposed should be determined as early as possible. Knowledge of these influences and intelligent appreciation of their effects are absolutely necessary to the success of oyster culture. Thousands of dollars would be annually saved to the Connecticut oystermen if they could determine, with even approximate accuracy, the date when the attachment of the young oyster would occur. Hundreds of thousands would be saved if they had any reliable method of determining the probabilities of the spawning season. Careful, continuous, and elaborate study and investigation alone can determine these points and others of equal importance. Considering the value of successful determination, not only in a scientific aspect, but practically, no effort or expense should be spared to obtain it."

Spawning.—Winslow (29, p. 130), Tangier and Pokamoke Sounds: "The spawning season was said to be from May until August inclusive, though most of the spawning was done in June and July." Brooks (5, p. 10): "Oysters in from 1 to 6 feet of water in the vicinity of Crisfield, probably spawn between the middle and end of May, but oysters with ripe eggs were found in water from 5 to 6 fathoms deep from the first to the thirtieth of July, although most of them spawn late in June." Ryder (7, p. 326): "In the region of the Chesapeake the most important spawning period seems to extend over the months of June and July, but considerable ripe spawn may be found even much earlier and later than this."

Growth of Larva.—Ryder (7, p. 328): "At a temperature of 75 to 80° F. the period of incubation of the American oyster is only 5 to 6 hours, when the young commences to live an independent active existence." "The duration of the locomotive stage of development of the larva has not yet been certainly determined . . . it has been found by the writer that under favorable circumstances attachment of the fry probably takes place within 24 hours after fertilization as represented at *m* in Fig. 1. The young, however, after attachment, continue to grow as larvæ . . . when the valves of the fry have acquired umbos the development of the spat shell begins." Ryder (9, p. 728): "I would infer from what we learn from the study of other animals that it may require quite a week before an embryo reaches

the dimensions of 1/80 of an inch, but we have no data upon which to base any conclusions of value.''

Spatting.—Rice (34, p. 115): '' The attachment takes place in about two days from the time of fertilization.'' Jackson (11, p. 532): ''One of the most successful spatting grounds at Buzzards Bay is a sand spit on South Wareham . . . oysters were spatting most abundantly late in July and early August.''

Growth of Spat.—Ryder (9, p. 728): ''After fixation the growth of spat is very rapid—week or 10 dys., $\frac{1}{4}$ inch across; 20 dys., $\frac{7}{16}$ in.; 44 dys., $\frac{13}{16}$ in.; 48 dys., 1 in.; 79 dys., $1\frac{3}{4}$ in.; 82 dys., 2 in.'' Ryder (7, p. 328), Figs. 5, 6, 7, etc.

Number of Spat.—Ryder (32, p. 287): ''As many as 25 young oysters might have been counted on a surface of one square inch'' on wooden buoys taken up early in July near Woods Holl. ''More than 100 oysters on a single shell.'' Rice (34, pl. 6, f. 12) figures the inside of an old oyster valve with 165 young attached. I never saw anything like such numbers at Malpeque—having to examine many shells to find one bearing one or two spat.

Output.—Winslow (30, p. 233) gives for the United States 22,195,370 bushels, of which 19,712,320 bushels came from Chesapeake and Delaware Bays. Kemp (42, p. 353) gives for Canada a table from which it is seen the maximum production was reached in 1882 of 64,646 barrels.

Breeding.—Rice (34, p. 115): ''The first efforts in this country in the direction of artificial propagation were made by the writer in the summer of 1878 in conjunction with Dr. W. K. Brooks, but these experiments were not successful. The next summer, however, Dr. Brooks succeeded in impregnating the eggs and in raising the embryos until they were six days old.'' Brooks (5, p. 3): ''. . . succeeded in raising countless millions of young oysters.''

Oyster Culture.—Under this head might be included an extensive literature dealing largely with the transplanting of oyster spat, that have escaped the accidents of nature, to more favorable localities as regards crowding, competition, food, cleanliness, etc.; but also to a more limited extent the breeding of larval oysters under artificial conditions that protect them against extremes of temperature, violent storms, starvation, rapacity of animals, etc., and the furnishing of abundant and suitable objects for fixation. The subject is too vast for discussion in this place.

It would appear that, to some extent simulating the life-history of the oyster, the short period of activity in investigation and experimentation initiated by Brooks was succeeded by a period of quiescence in research, when statements were repeated but not examined anew. Deliberate, painstaking, self-reliant, and unbiased work, like that of Nelson (37), may do much to originate a new cycle of exact observation, which sooner or later may be turned to account in a rational system of oyster culture.

MONTREAL, May 18, 1909.